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J. Zool., Lond. (2003) **261**, 345–351 © 2003 The Zoological Society of London Printed in the United Kingdom DOI:10.1017/S0952836903004308

Communal nesting in the usually solitary marsupial, *Phascogale tapoatafa*

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(Accepted 20 May 2003)

Abstract

The marsupial brushtailed phascogale *Phascogale tapoatafa* is a solitary, hollow-dependent, arboreal insectivore that occurs at low densities in open forests and woodlands of Australia. Data gathered from nest box surveys (4 years), and from radio-tracking phascogales to nest sites (3 years) in south-western Australia confirm solitary nesting after dispersal. However, in the winter of a single year, nest box surveys in one study area showed that 56% of individuals were nest sharing. On a neighbouring site, 81 group nests were also recorded among 18 radio-collared individuals. In both areas, groups comprised two to four individuals of any age/sex combination. The same phascogales tended to nest together and in a number of different sites. Nest sharing between females was restricted to territory boundaries and continued after the annual die-off of the males. Nest sharing coincided with prolonged drought conditions and in this year mature phascogales were significantly smaller than normal, i.e. males 25% less in weight, females 12% less. Communal nesting seemed to be a response to thermoregulatory difficulties posed by the three interrelated factors of low body mass, declining temperatures and declining food availability. Nest sharing in this species appeared to be a behavioural indicator of an energetics crisis, there was a population decline during the drought period and a population crash in the following year.

Key words: brushtailed phascogale, *Phascogale tapoatafa*, nesting behaviour, nest sharing, communal nesting, thermoregulation

INTRODUCTION

Group nesting or increases in group size over winter, as a way of conserving energy, have been concluded or reported for several small eutherian mammals, e.g. voles (Wolff & Lidicker, 1981; Madison, 1984; McShea & Madison, 1984), squirrels (Muul, 1968; Koprowski, 1996) and bats (Herreid, 1963). Such behaviour is also observed among some Australian marsupials, sugar gliders *Petaurus breviceps* (Henry & Suckling, 1984), feathertail gliders *Acrobates pygmaeus* (Frey & Fleming, 1984), and fat-tailed dunnarts *Sminthopsis crassicaudata* (Morton, 1978*a*,*b*). Either the huddling associated with group nesting increases actual body temperature, or animals are able to maintain their normal temperature at a lower metabolic cost (see Muul, 1968; Withers & Jarvis, 1980). However, it is difficult to conclude that communal nesting serves only a thermoregulatory/energetics role when animals are normally social, maintain group and family bonds or nest together in all seasons. This interpretation is also confounded when aggregations are associated with mating and breeding activities that occur in winter (e.g. *Antechinus*, Lazenby-Cohen, 1991; Cockburn & Lazenby-Cohen, 1992).

Several advantages of group nesting, other than thermoregulation, have been proposed and these largely follow the reasons given for social grouping by Alexander (1974). These include suggestions that grouping may increase predator avoidance/defence, increase food acquisition, and that tolerance of social grouping allows the exploitation of localized resources. However, the converse are also given (summarized in Alexander, 1974) as possible reasons why animals do not aggregate or nest socially; increased predation risk, food competition, and also increased chance of parasite transmission.

Solitary nesting is documented as typical for the brushtailed phascogale *Phascogale tapoatafa* (hereafter phascogale) in Victoria (Soderquist & Ealey, 1994). It was also found to be the usual nesting behaviour during the first 3 years of this study of wild phascogales in south-western Australia. However, in the fourth year of the research nest sharing was common. No a priori reason existed to question the species solitary nature, and the information presented was gathered while pursuing other aspects of the study.

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The brushtailed phascogale is a small marsupial. It is a squirrel-sized arboreal insectivore found throughout open forests and woodlands of mainland Australia (Soderquist, 1995*a*). The species is rarely encountered during routine faunal surveys and typically occurs at low densities. Females occupy intrasexually exclusive territories of large size (e.g. *c*. 41 ha) while male home ranges (average 106 ha) overlap with both sexes (Soderquist, 1995*b*). Phascogales have an annual life-history strategy with sexual maturity being reached at 1 year of age and all the males die after the winter mating period (Cuttle, 1982; Lee & Cockburn, 1985). Females are monoestrous and take 5 months to raise their young to weaning. A proportion of the females survive to breed in a second year (Soderquist, 1993*a*; Rhind, 2002).

METHODS

General background

Phascogales in south-western Australia were studied between 1992 and 1997. As the species had not previously been investigated in Western Australia, the initial aims of the research were to determine general biological, reproductive and behavioural characteristics. The latter stages of the work explored the impacts of forestry practices.

The study was conducted in open dry sclerophyll forest 350 km south of Perth (34°10′S, 116°35′E). A characteristic of this region is its Mediterranean climate (cf. south-eastern Australia), and it experiences particularly long dry summers where rain is absent for 5–7 months; the winters are cool and wet with rainfall peaking in June–July (Gentilli, 1989).

The sites used for the study (each 200 ha) included 2 in the Perup Nature Reserve, and 3 in the Kingston Forest located 20 km from Perup. The Perup sites were used to collect general information about the species, while the Kingston sites were specifically established to investigate the impacts of a logging operation. An additional site, midway between these 2 areas, was used for a few months in 1994 to examine the effects of a controlled burning exercise.

Phascogales were caught both by trapping and by using nest boxes. Recapture success with this species is poor, so monitoring was undertaken by radio-tracking. The capturing, handling, measuring and radio-collaring methods are described in Rhind (1998, 2002) and Rhind & Bradley (2002). The research activities for each year were carried out between the time that the young dispersed (December/January) and the beginning of the breeding period (July/August). All males disappeared (died) around July, which resulted in a population decline each winter. Young phascogales reached a weight suitable for radio-collaring shortly before dispersal (December).

One of the research aims was to investigate the species refuge requirements by identifying the locations, characteristics, number and frequency of use of nest sites. Three other aspects of the research also captured information about nesting behaviour (although were undertaken for different reasons), and these 4 different sources of data (described below) are used to address the social nature of phascogale nesting behaviour.

Radio-tracking and nest box surveys

First, the study of refuge sites was carried out by radio-tracking phascogales to their day-time nest sites. The term ‘nest site’ is chosen to describe phascogale refuge sites because the species builds nests, and does so at all times of the year (Traill & Coates, 1993; Soderquist *et al*., 1996; Rhind, 1998). Approximately 140 phascogales were radio-tracked to nest sites between late 1992 and August 1995. Individuals were typically collared for up to 1 month, and located at their nest sites every day. During 1995 (see below) tracking periods were more extensive.

In this low density population the potential to detect nest sharing using radio-tracking techniques, even with intensive tracking, is limited by the proportion of the population that is collared in a local area. The highest densities of collared animals were achieved in 1994 and 1995 so detailed radio-tracking data presented in the Results are restricted to these 2 years.

Second, phascogales were captured by using nest boxes. By mid-1993, nest boxes were erected on the 5 study sites at a density of *c*. 1 box per 9 ha ($n = 170$ boxes) and these were checked a total of 2052 times. Field research on this species ended in August 1995, but the boxes were checked again in January and March 1996, and in January 1997. All nest boxes were used by phascogales, none was used by other mammal species, and *c*. 50% of the 387 individuals caught during the study were captured using this method.

To illustrate the general absence/presence of nest sharing in nest boxes, all results from the nest box surveys (1992–97) are presented, and are given by month with all sites combined. The effort of checking nest boxes varied between the months, years and sites, but similarly timed checking was undertaken on the Kingston sites between January and April for 3 years of the study. Averaged capture rates from that period are used to describe differences in phascogale abundances between years.

Third, phascogales were radio-tracked at night to investigate foraging behaviour and to determine territory/home-range sizes. This work provided information of the location of nests in relation to phascogale territory boundaries. The radio-tracking methods used are described in Scarff, Rhind & Bradley (1998) and, in brief, involved tracking directly to the phascogale, observing its behaviour and recording its location. A 3-h interval was imposed between successive fixes on the same individual. The Wildtrak non-parametric home-range analysis package (Todd, 1992) was used to analyse this information and both night fixes and nest locations were included in the data. The minimum convex polygon method (MCP) (Mohr, 1947) was chosen to define territory sizes as it provided results comparable to other

studies, including the phascogale study by Soderquist (1995*b*).

Finally, systematic behavioural observations of phascogales were undertaken between December 1992 and February 1994. That study involved 30-min focal follows of individuals (Altmann, 1974) resulting in approximately 100 h of observations of 32 phascogales (see Scarff *et al*., 1998). The follows typically began and ceased at a nest site, and hence incorporated direct observations of the number of phascogales using a particular site.

1995 research

In the year that communal nesting was observed, research activities were focused on an investigation of the direct affects of logging on phascogales. By the time nest sharing was first detected in March 1995 (2 Kingston sites), intensive radio-tracking was confined to the 1 Kingston site that was being logged. The radio-tracking results that describe nest sharing in 1995 were obtained on this single site.

Between 1 January and July 1995, 23 phascogales were radio-tracked on this site for between 20 and 131 days (21–143 days collared per individual). Logging occurred between February and June. Nine females were sufficiently radio-tracked to determine their territory parameters and so identify the locations of shared nests in relation to territory boundaries. Males are not territorial (Soderquist, 1995*b*; Rhind, 1998) so the spatial arrangement of their nest sites were excluded from examination. Systematic behavioural observations were not part of the work undertaken in 1995, however phascogales on this site were regularly observed at night, including around their nest sites.

In 1995, nest boxes were checked on all 5 study sites before phascogale dispersal (December 1994) and many young were captured with their mothers (Rhind, 2002). This allowed identification of relatedness for some of the females subsequently found nest sharing later in the year. Detailed results of nest box sharing in 1995 are confined to those gathered on the Perup sites as these data are independent of the radio-telemetry-based information given for the Kingston area. This separation of information is especially important because the Perup sites were not influenced by logging activities.

RESULTS

Radio-tracking

Between December 1992 and August 1995, 4459 nest site locations were identified; these were recorded as one occupied site, per individual, per day. Phascogales nested in tree hollows or nest boxes, and the specific tree in use was identified in *c*. 95% of radio-tracking cases (Rhind, 1998). The hollows themselves were rarely located. Excluding mothers with dependent young, phascogales most commonly used the same nest site for 2–5 days before moving to another (Rhind, 1998).

Table 1. Number of times groups of radio-collared phascogales *Phascogale tapoatafa* were found sharing nests on the Kingston study site, 1995

Months	March	April	May	June	Total
Frequency	3	17	39	22	81

In 1994 and 1995, 2167 radio-tracking locations to nest sites were obtained during summer/early autumn (December to mid-March). The only incidence of observed nest sharing was that recorded between two dispersing sisters. These females nested together in one tree on 13 occasions during January to February 1994. The shared tree was located on the boundary of their neighbouring territories. Excluding these individuals and dependent family members, single phascogales were observed leaving or entering the same refuge site during *c*. 100 h of systematic behavioural observations (1992–94) conducted during the study.

Before March 1995, radio-tracking indicated solitary nesting after dispersal and before winter. However, a few instances of females sharing nest location were observed in winter 1994. One pair nested in the same tree on nine occasions and another pair was opportunistically observed sharing a nest box.

In contrast, 81 group nests were identified among radio-collared phascogales on the Kingston site in 1995 (Table 1). Nest sharing was first observed on 17 March. Between then and 28 June (when male die-off became apparent), the phascogales on this site were radio-tracked on 93 days and locations of 810 nest sites were recorded. Communal nesting was observed on 49% of these days with 174 (24%) of nest site records scored as a site containing more than one individual. Uncollared phascogales were undoubtedly present, so nests recorded with only one collared animal may also have contained other phascogales.

The daily percentage of radio-tracked individuals found sharing nests is presented in Fig. 1. As 63% of the nest sharing events occurred in nest boxes, phascogales located to the same tree were presumably occupying the same hollow.

Shared nests contained two or three collared phascogales (Table 2). Groups of two were of any sex combination, and groups of three contained both sexes. Relatedness between most of these phascogales was unknown, but one nest was shared several times by a second year female and a first year female who were not mother and daughter. Females shared nests together on nine occasions, and these sites were situated on the periphery of their otherwise exclusive territories (Fig. 2).

Several individuals shared nests on consecutive days and/or returned to nest together after nesting apart. Two group alliances were particularly marked. One pair of males nested together on 25 days; they also nested together once, and singularly, with the same female on

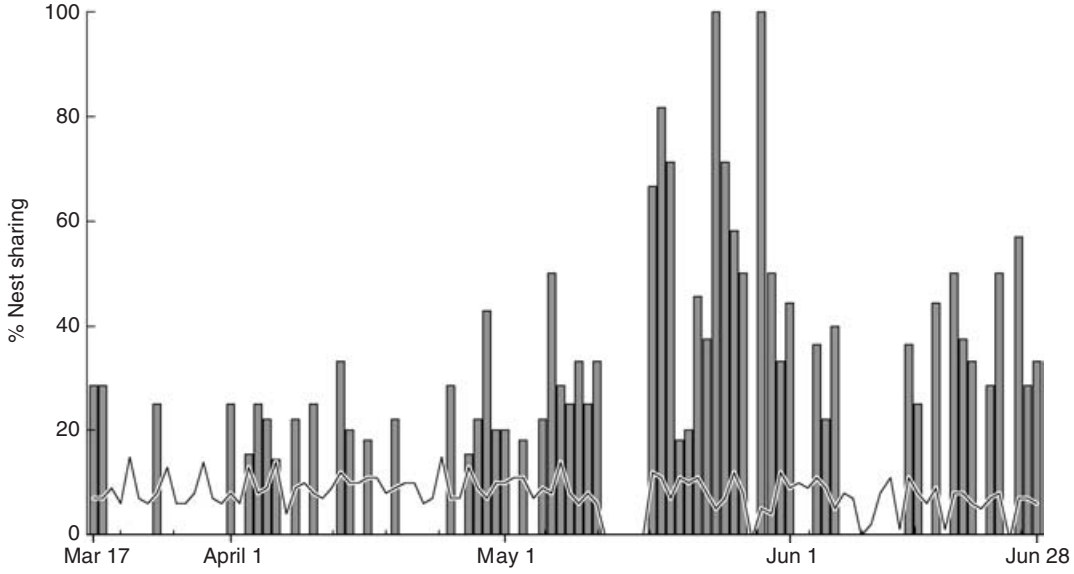

Fig. 1. Daily percentage of radio-tracked phascogales *Phascogale tapoatafa* found sharing nests; Kingston site 1995. Line, number of individuals tracked each day.

Table 2. Frequency, sex and number of phascogales *Phascogale tapoatafa* identified in shared nests; results based on radio-tracking observations at the Kingston study site, 1995

Group composition	Frequency
Female + female	8
Female + male	30
Male + male	31
Female + female + male	1
Female + male + male	11

12 occasions in three different nest sites. A few days after this female was killed (presumably by a fox), the males ceased using the sites they had shared with the female. In addition to nesting apart they continued to nest together in three other sites until they died of natural causes around 8 July. Another group of three phascogales was found together in various combinations on 18 days. One of these males travelled 1.2 km (line-of-sight) between nest sites, sometimes overnight, to reach the communal nests. Logging on this site was patchy and nest sharing was observed both among those phascogales that were directly impacted by logging, and among those that were not.

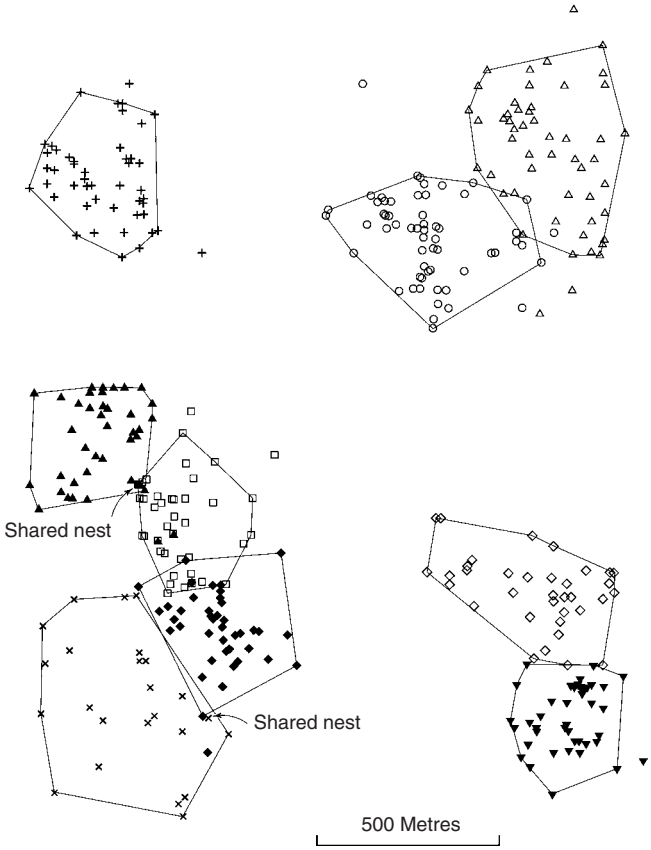

Fig. 2. Territories of nine female phascogales *Phascogale tapoatafa*, Kingston site, 1995. Each female is represented by a different symbol; each occurrence of a symbol illustrates a night (foraging location) or day (nest location) radio-tracking fix. Nest sites that were repeatedly used are shown only once. Territory boundaries based on the 95% minimum convex polygon method (Mohr, 1947).

Nest box surveys

A total of 139 phascogales were captured from nest boxes in summer/early autumn (1 January and April 18) during 1993 to 1997. All but one box contained a single animal (Table 3). During mid-autumn/winter (mid April–July), 48 phascogales were captured from nest boxes and none was found sharing during 1992–1994.

In contrast, in 1995 nest sharing was common for this same autumn/winter period. On the Perup sites (which

Table 3. Number of phascogales *Phascogale tapoatafa* found occupying nest boxes (all study sites combined). Bold, total number of individuals observed sharing nest boxes; other boxes contained single occupants

Month	1992	1993	1994		1995		1996	1997
January	–	5	7		5		7	11
February	–	3	41	2	16		–	–
March	–	9	–		16		11	–
April	–	3	13		27	5	–	–
May	3	10	1		16	4	–	–
June	1	1	6		40	18	–	–
July	1	3	6		19	7	–	–

Table 4. Frequency, sex and number of phascogales *Phascogale tapoatafa* found sharing nest boxes in 1995 at the Perup study sites

Dates of nest box surveys	Group composition	Frequency
Before male die-off		
26 April–18 June	Female + female + male	4
	Female + male + male	1
	Male + one?sex	1
	Female + female + male + male	1
After male die-off		
22–31 July	Female + female	2
	Female + female + female	1

were not affected by logging) 10 of 32 occupied nest boxes contained more than one phascogale, and 56% of the 50 captured phascogales shared nest boxes. Groups consisted of two to four individuals, contained both sexes before male die-off, and females continued to share nest boxes after die-off (Table 4). Relatedness was known for a few of the females and on three occasions the same mother/daughter pair were found together. One first year female nest shared with a second year female who was not her mother.

Climate, phascogale condition and abundance

Nest sharing in 1995 coincided with the temperature decline in autumn (March), and monthly minimum temperatures seemed to be similar in 1994 and 1995 (Fig. 3). Rainfall, however, varied markedly during the study and progressively declined throughout the research, with the most severe drought on record occurring in 1994 (discussed in detail in Rhind, 2002; Rhind & Bradley, 2002). In that year the area received 30% less rain than average and phascogales raised during this time were small at weaning and did not reach normal size as adults in 1995 (Fig. 4). At maturity (mid 1995) these phascogales were significantly smaller in skeletal measures and weighed an average 25% (males) and 12% (females) less than phascogales caught in 1994 (Rhind & Bradley, 2002). In comparison to male phascogales in Victoria (see Fig. 4),

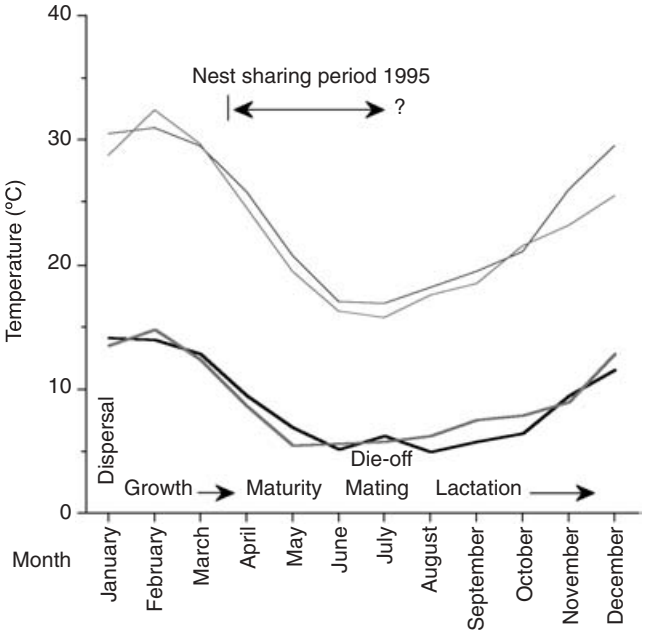

Fig. 3. Minimum and maximum monthly temperatures for the study area; 1994 and 1995. Phascogale *Phascogale tapoatafa* life-history phases and behaviours are shown for context. Monitoring of phascogales ceased in early August 1995 so it is unknown whether nest sharing continued beyond this time.

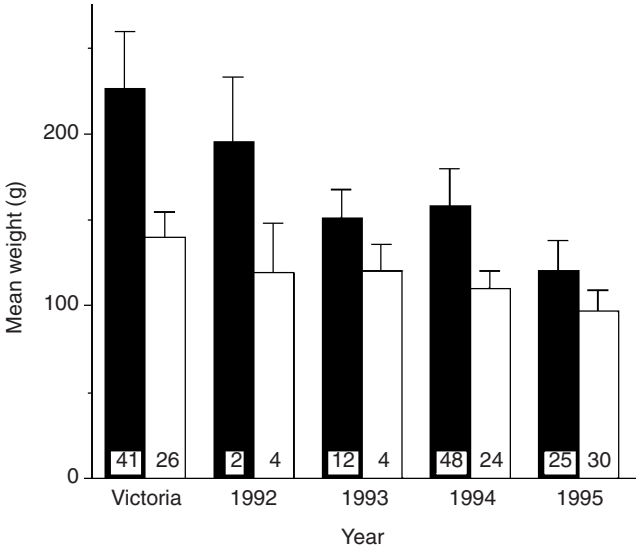

Fig. 4. Mean weights (± standard deviation) of first year mature phascogales *Phascogale tapoatafa* (captured after 1 May in each year) for 4 years of the study; males (black), females (white); sample sizes indicated. Comparable weights of mature Victorian phascogales were derived from data provided by T. Soderquist (pers. comm.).

the 1995 males achieved half the mass of their south-eastern Australian counterparts.

Phascogale mortality seemed to be high in late 1994 and throughout 1995 (Rhind, 1998), and few phascogales were captured in 1996. An average 21% of the nest boxes at the Kingston site were occupied by phascogales in early 1994

and 1995, compared to 7% (Kingston) and 5% (Perup) occupancy rates in 1996.

DISCUSSION

This study documented extensive autumn/winter communal nesting in a mammal species that usually nests alone at all times of the year. Such a behavioural change does not seem to have been reported before in a solitary mammal species. Indeed, there are only two well-documented accounts of shifts to social winter nesting among species that are solitary at other times of the year. Flying squirrels *Glaucomys volans* routinely share nests in winter (Muul, 1968), and fat-tailed dunnarts *S. crassicaudata* form winter nests not only with each other, but also with mice *Mus musculus* (Morton, 1978*a*,*b*). Both of those studies concluded that this behavioural change was undertaken for energy conservation. Unlike these two examples, the field data gathered so far on phascogales suggest that nest sharing is rare at any time of the year (this study; Soderquist, 1995*b*). The extensive winter communal nesting observed in this species seemed to be a single year anomaly.

A range of evidence was gathered during this work to suggest that the nest sharing was related to energetics difficulties. There is little to support the idea that this behavioural shift conferred any social benefits (as summarized by Alexander, 1974) such as improved food acquisition or vigilance against predators. This insectivorous species forages alone, does not socially gather or store food, and outside the nest, phascogales are indifferent or hostile to other phascogales (Traill & Coates, 1993; Soderquist & Ealey, 1994; Rhind 1998; Scarff *et al.*, 1998). More specifically, nest sharing between the females occurred on the peripheries of their territories so foraging ranges were not shared among females. It is also unlikely that communal nesting was related to reproductive imperatives such as mate familiarization (Lazenby-Cohen, 1991; Cockburn & Lazenby-Cohen, 1992) or mating (see Soderquist & Ealey, 1994). Nest sharing began 3 months before the mating period, occurred between same-sex individuals, and continued among the pregnant females after the males had died.

During these observations in 1995, phascogales were under the effects of protracted drought conditions. They were physically small and underweight, which was undoubtedly a consequence of low invertebrate food availability (Rhind & Bradley, 2002). However, this poor physical condition alone does not explain the shift from solitary to communal nesting. Weights of immature phascogales in the early months of 1995 were atypically low for the time of year (Rhind & Bradley, 2002), but no nest sharing occurred during this time. Also, in this year the few second year females present in the population also shared nests, but they were of the same average weight as second year females caught in other years (t-test, $t26 = 1.53$, $P = 0.14$).

The reason for and the timing of the shift from solitary to communal nesting is best explained by energetics problems brought on by the winter decline in food availability. In this region invertebrate abundance/activity shows a marked autumn/winter trough, and a concurrent study of invertebrate communities in and around the Kingston area suggested that these were negatively impacted by the 1994 drought (Strehlow *et al.*, 2002). Alternative mechanisms for conserving energy during such hard times do not seem to be available to phascogales. Several small marsupials can use torpor to conserve energy in winter, or when they are food deprived (e.g. Morton, 1978*a*; Fleming, 1980; Frey & Fleming, 1984). Torpor was not observed in phascogales caught during this study (*c*. 800 captures), nor was it reported among phascogales in Victoria (Soderquist, 1993*b*).

The nest sharing combinations found among the phascogales suggest that they were forming communal nests in a random way reflecting their social structure (Soderquist, 1995*b*), dispersal patterns (Soderquist & Lill, 1995) and low density. All age, sex, and relatedness combinations were identified. By default, in order to nest share, an individual would need to nest with what ever phascogale shared/neighboured its area otherwise it would be severely restricted in nest sharing options. The extent of regular sharing observed among some groups of radio-tracked individuals, including the distance travelled between sites (1.2 km in one case) probably signifies the limited availability of nesting mates.

This study confirms that solitary nesting is typical for phascogales following dispersal, and apparently this is true regardless of their physical condition or the environmental conditions. Some caution is needed, however, in generalising about winter nesting behaviour for this species in the south-west of Australia. Phascogales in Western Australia are considerably smaller in body mass than those in Victoria (Rhind & Bradley, 2002), and this seems to be linked to low food availability in the south-west jarrah forest (see Scarff *et al*., 1998; Rhind, Bradley & Cooper, 2001). Poor years in this already food-limited environment may mean that winter energetics difficulties arise more commonly than in other areas. Perhaps there is a critical threshold in food availability, temperature and body mass (somatic reserves) that culminate in a situation that triggers phascogales to nest share. If this is the case, 'winter' nest sharing may occur in some years and not others, and may start at different times in different years.

Nest sharing among phascogales presumably conferred survival advantages, but it is rather difficult to view this behavioural flexibility as an effective adaptation to harsh conditions. The study population declined markedly during and following these observations. Given this, nest sharing in this species is best interpreted as a 'last resort' survival tactic and a measurable indicator of marginal survival conditions for this normally solitary species.

Acknowledgements

Considerable support was provided to this project by J. Stuart Bradley, Todd Soderquist, volunteer field

assistants and staff of the Department of Conservation and Land Management at Manjimup. Clive Hilliker and comments by referees aided manuscript presentation and revision. The research was undertaken while a post-graduate of Murdoch University in receipt of an Australian Commonwealth Postgraduate Scholarship, and it was partially funded by an Australian Research Council grant.

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